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冻融作用对土壤呼吸影响的研究进展

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摘要：冻融作用对土壤呼吸的"激发效应"被证实在高纬度及高海拔地区普遍存在。气候变暖背景下，这些区域将经历更为频繁的冻融变化，并可能提高土壤呼吸对区域碳循环的贡献。本文概述了冻融作用对土壤呼吸的"激发效应"，从土壤物理性状、根系周转、微生物活性及群落结构等方面阐述了冻融作用对土壤呼吸的影响机制。未来研究需要：① 强化对高海拔生态系统的研究；② 注重将原位观测与室内冻融模拟相结合，并进一步优化室内模拟实验；③ 综合考虑生物及非生物因子影响；④ 从土壤呼吸组分的角度探究土壤呼吸对冻融变化的响应机理。

关键词：土壤呼吸；冻融变化；激发效应；生物因子；非生物因子

土壤呼吸是陆地生态系统碳输出的主要途径，由环境变化引起的土壤呼吸强度的微弱改变都有可能对生态系统碳平衡产生显著的影响[1-3]。土壤冻融是由季节或昼夜热量周期变化使土壤交替出现冻结-融化的过程，其作为一种自然现象普遍存在于高纬度及高海拔地区[4-5]。冻融作用不仅直接改变了土壤水热条件，而且深刻影响着土壤理化性状[6-7]、微生物与酶的活性[8-9]、根系周转[10-11]。冻融期间土壤所经历的一系列物理、化学、生物变化过程将导致其物质能量循环过程及速率发生变化[12-14]。

近年来，大量研究表明，冻融作用对土壤呼吸有着不可忽视的影响，冻融期土壤呼吸在年土壤呼吸总量中占有重要比例，并显著地影响着生态系统碳收支[15]。目前，有关土壤呼吸的研究主要集中于生长季，而对非生长季，尤其是冻融期土壤呼吸过程的研究相对滞后[16]。土壤冻融过程普遍发生的高纬度及高海拔地区往往是对全球变暖响应较为敏感的区域[17]，在气候变暖的背景下，这些区域将经历更为频繁的冻融变化[18-20]，并可能对土壤呼吸产生"激发效应"，提高土壤呼吸对区域碳循环的贡献[21-22]。因此，系统研究土壤呼吸过程对冻融变化的响应机制，对于精确评估生态系统碳收支具有重要意义。本文概述了冻融作用对土壤呼吸的"激发效应"及主要影响因素，并从土壤物理性状及通气性、根系的周转、微生物活性及群落组成等方面系统阐述了冻融作用对土壤呼吸的影响机制；探讨了当前开展相关研究方法中的不足及需要改进的方向；最后，结合目前的研究进展，指出了未来的研究重点。

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1 冻融作用对土壤呼吸的“激发效应”及主要影响因素

近年来，在极地苔原、泰加林、高寒草甸及沼泽湿地等极地及温带生态系统的研究表明，在融化期土壤呼吸往往会出现大幅增加的现象，冻融期土壤呼吸最高可占到全年土壤呼吸总量的 50%以上[23-27]。许多学者将这一现象称为冻融作用对土壤呼吸的“激发效应”[21,28]。鉴于冻融作用对土壤呼吸过程的重要影响，土壤呼吸对冻融变化的响应已成为当前土壤碳循环研究领域的热点问题[29-30]。

虽然冻融作用对土壤呼吸的“激发效应”被证实在生态系统中普遍存在，但对于不同生态系统，土壤呼吸增加的幅度存在较大差异。Vestgarden 和 Austnes[31]在挪威泥炭地的模拟冻融研究中发现，冻融处理后土壤呼吸速率平均提高 48%；而对于某些极地苔原及高山苔原生态系统，土壤呼吸速率增加的幅度可达 50 倍以上，出现明显的峰值[29]。相较于苔原生态系统，森林生态系统在冻融期一般具有较高的土壤呼吸速率[15]；一些在温带森林的研究表明，融化期森林土壤呼吸速率也会数倍增长，并可持续较长时间，出现多个明显的排放高峰[26,32]。

冻融期土壤呼吸的变化还受冻结温度、冻结前土壤水分含量、冻结时长等因素的影响。Neilsen 等[33]最早采用模拟冻融实验研究了北方森林土壤呼吸对冻结温度变化的响应，发现冻结温度为-13 ℃的土壤在融化期排放的 CO_2 显著高于冻结温度为-8 ℃的处理，而冻结温度为-8 ℃ 的土壤在融化期排放的 CO_2 又高于冻结温度为-3 ℃的处理。此后，Goldberg 等[34]及 Wei 等[26]在挪威云杉林及我国东北落叶松林也发现，冻结温度越低，融化期土壤呼吸速率越高。针对冻结前土壤含水量变化对冻融期土壤呼吸过程的影响，Wu 等[35-36]及褚建民等[37]对森林、草地、沼泽、农田等典型生态系统的研究表明，在高含水量条件下土壤呼吸速率均显著高于低含水量，但是有关冻融过程中土壤水分变化对土壤呼吸的作用机制还不明晰。这些研究还发现，随着冻结时间的延长，土壤呼吸越容易在融化期出现峰值。冻融循环次数也是影响土壤呼吸过程对冻融变化响应的重要因素[5]。有研究发现，在前几次冻融循环的融化期土壤呼吸一般都会出现明显的峰值，但是随着循环次数的增多，土壤呼吸速率增加的幅度逐渐减小直至稳定[38-40]。一般认为，冻结温度越低，冻结时间越长，冻结前土壤水分含量越高，土壤呼吸越容易在融化期出现峰值，但随着冻融循环次数的增加，土壤呼吸增加的幅度会逐渐降低。

土壤冻融通常伴随着降雪过程。积雪厚度及持续时间的变化可以通过改变表层土壤温度，增加或减少冻融循环次数，影响冻融期土壤呼吸速率[15,32,41]。杨开军等[42]在川西亚高山云杉林的雪被去除实验发现，雪被去除加大了土壤温度的波动幅度，使冬季表层土壤冻融循环增加了 39 次，土壤呼吸速率降低了 21.02%；而 Li 等[43]基于 meta-analysis 研究发现，雪被厚度增加后土壤呼吸速率平均增加了 15.5%。朱新萍等[44]在高寒湿地及农田也观测到了类似现象。同时发现，积雪持续时间越长，融化期土壤呼吸速率增加的幅度越大，但是排放峰值会滞后。当前有关冻融作用对土壤呼吸影响的研究多集中于中高纬度地区，而对多年冻土

和季节冻土广泛分布且对气候变化响应敏感的高海拔地区的研究相对缺乏。

2 冻融作用对土壤呼吸的影响机制

土壤呼吸主要由微生物呼吸和根系呼吸组成[45-47]。一般认为冻融作用可通过改变土壤物理性状及通气性、根系的周转、微生物活性及群落结构[9,39,48]影响土壤呼吸。

2.1 冻融作用对土壤物理性状的影响

冻融作用通过对土壤物理性状的改变主要从以下方面影响土壤呼吸：（1）土壤颗粒在冻结时表面会形成冰膜，阻碍了由土壤微生物代谢和根系自养呼吸产生的 CO_2 向外扩散而聚积在土壤中，并在融化期时形成排放的高峰[35,49]；（2）土壤孔隙中液态水冻结成冰时，体积膨胀，破坏了土壤团聚体结构，随之释放出大量的可被微生物利用的活性有机碳，从而导致土壤呼吸速率增加[5,50]。一般而言，冻融作用能够破坏土壤结构，影响团聚体稳定性，其破坏程度主要与土壤含水量、冻结温度和冻融循环次数、团聚体大小有关[51-55]。土壤冻融过程的实质是由温度变化引起的土壤水分相变，因此冻融作用对团聚体的影响与土壤含水量、温度密切相关。Wang 等[56]的研究表明，相同温度条件下，达到饱和含水量时冻融作用对团聚体破坏性最强；相同含水量条件下，团聚体稳定性与温度呈二次函数关系。徐俏等[57]的研究也发现，冻融过程中土壤含水量是影响团聚体稳定的重要因素，且随着含水量的提高，粒径>2 mm 的水稳性团聚体呈现降低的趋势，而粒径<1 mm 的团聚体呈现增加的趋势。Li 等[55]研究发现冻融作用可将土壤大团聚体破碎成小团聚体，并且冻结温度越低、冻融循环次数越多，其对大团聚体的破碎作用越明显。Xiao 等[58]进一步发现冻融作用对土壤团聚体的破坏主要源于参与团聚体形成的球囊霉素等疏水性糖蛋白含量的降低。此外，冻融作用还可以增加土壤的孔隙度，提高土壤通气性，促进融化期 CO_2 排放[59]。

2.2 冻融作用对根系周转的影响

冻融作用对根系最直接的影响是使根系遭受物理伤害而凋亡，死亡根系分解时会增加土壤中可被微生物利用活性底物的含量，促进土壤微生物呼吸[11,60-62]。Cleavitt 等[10]和 Tierney 等[62]在美国次生阔叶林的研究证实了上述认识，并测算出冻融期细根的凋亡可导致超过 1.5 $g\ C{\cdot}m^{-2}$ 及 0.5 $g\ N{\cdot}m^{-2}$ 的养分释放。Wu 等[63]在川西云杉林的原位研究进一步表明，冻融作用不仅提高了细根的凋亡率，而且可以通过促进死亡细根 C、N、P 和 K 等元素的释放在冻融后期提高根际微生物活性，促进细根残体的分解。冻融作用还可以通过改变细根的生长过程影响根系自养呼吸。冻融作用对根系生长过程的影响主要表现在以下方面[11,64]：（1）冻结会阻碍根-土界面水分及营养元素的交换，使得部分根系由于受到水分、养分的限制而难以正常生长；（2）土壤冻结时，根系无氧呼吸占主导，由无氧呼吸产生的有害分泌物的积累会对根系的生长产生抑制作用。由于土壤冻结对细根生长的抑制，冻融作用对根系自养呼吸的激发作用有限[11]。

2.3 冻融作用对微生物活性及群落结构的影响

冻结与氯仿熏蒸、干湿交替等过程一样也会造成土壤微生物死亡，死亡的微生物释放出的 C、N、P 等营养物质会提高存活微生物的活性，促进融化期土壤微生物呼吸[65-69]。有研究发现，1 次冻融循环能导致超过 50%的微生物死亡[40]。Herrmann 和 Witter[38]借助 ^{14}C 示踪技术发现，融化期土壤排放的 CO_2 中有 65%源于微生物残体。此外，由冻融作用引起的团聚体的破坏及细根凋亡释放的活性有机碳将进一步提高土壤中可被微生物利用的底物含量，增强微生物活性。高珊等[70]对长白山主要温带森林的研究发现，经多次冻融交替作用后表层土壤微生物活性和数量均有明显提高。也有研究表明，由于对低温的适应，高寒地区土壤微生物可对冻融循环表现出一定的适应性[71]。

冻融过程还会对土壤微生物的群落结构产生重要影响[5,72]。Kreyling 等[11]基于高通量测序方法发现，冻融作用显著提高了真菌的活性，尤其是腐生菌类的活性。刘利等[73]对川西亚高山森林研究发现，经多次冻融循环后表层土壤细菌数量及多样性均显著降低。Ollivier 等[74]及 Juan 等[75]进一步发现，冻融作用还能导致特定细菌功能群发生变化，对微生物的功能性状产生重要影响。总体来说，冻融作用能导致土壤微生物群落由以细菌为主导转变为以真菌为主导[76-77]。真菌的碳同化效率高于细菌，即代谢时能同化更多的碳，释放更少的碳；且真菌细胞壁主要成分为碳聚合物，相较于细菌细胞壁（主要成分为肽聚糖、磷脂）更难分解[78-80]。因此，以真菌为优势群落的生态系统的土壤呼吸速率一般相对较低[80-82]。冻融作用下土壤微生物群落由以细菌为主导向以真菌为主导的转变将不利于融化期 CO_2 排放高峰的形成。

3 开展冻融作用对土壤呼吸影响研究的主要研究方法

原位观测和室内冻融模拟是开展冻融作用对土壤呼吸影响研究的主要手段[4,29]。原位观测一般对野外实验平台要求较高，且容易受到环境因素的干扰[83]，而室内模拟冻融实验由于成本低、可控性强，是目前较为常用的方法[40]。室内模拟实验通常采用培养箱或冰箱对供试土样进行温度控制来实现土壤冻融模拟[4,5]。由于土壤所处的冻融环境与自然状态存在明显的区别，研究结果易受到采样时间与方法、温度变化的幅度、冻融周期的长短、循环次数等因素的影响。因此，开展室内模拟冻融时需注意如下方面，以贴近自然条件[4-5]：（1）土壤微生物及根系周转具有明显的季节变化特征[10,76]，春夏季采集的土壤由于刚经历完冻融循环，培养结果可能与秋冬季采集土壤不同[40]，因此，模拟冻融实验所需土壤样品应在秋冬季采集；（2）自然条件下气温变化是个缓慢的过程，因此，进行室内培养时应避免因温度的急剧变化而导致土壤微生物的快速死亡[83]；（3）自然条件下土壤冻结和融化时温度的变化都是自上而下，因此，室内培养时应尽可能保证土壤温度从表层开始变化[26,31]；（4）冻融模拟时应考虑土壤表层覆盖的积雪和凋落物，因为积雪和凋落物一方面可以对温度变化起到缓冲作用，另一方面会影响融化期土壤含水量及养分含量的变化[42-43]；（5）现有的研究中冻融周期的设计时长一般为 1～2 d，冻融循环次数一般低于 5 次，远小于野外实际情况。

因此，在条件允许的情况下，室内模拟冻融周期及冻融循环次数应尽可能增加。尽管室内模拟冻融存在缺陷，但仍是研究土壤呼吸对冻融变化响应机理的主要手段，同时也是对原位研究的重要补充。将野外原位研究与室内模拟冻融相结合，能实现优势互补、相互验证，从而有助于更加准确深入的理解冻融作用对土壤呼吸过程的影响机制。

4 研究展望

综上所述，关于土壤呼吸对冻融变化响应的研究将表现如下发展趋势：

（1）国内外相关的研究多集中在极地苔原、北方森林、泥炭地、沼泽湿地等中高纬度生态系统，而对多年冻土和季节冻土广泛分布且对气候变化响应敏感的高海拔生态系统的研究相对薄弱，需强化对高海拔低温生态系统土壤呼吸过程对冻融变化响应的研究。

（2）受到研究手段限制，目前关于土壤呼吸对冻融变化响应规律的认识存在较大分歧，后续应注重将原位观测与室内冻融模拟相结合，并进一步优化室内模拟实验方案，以贴近自然条件。

（3）土壤呼吸对冻融变化的响应是一个多因素影响的综合效应过程，积极探索新的研究思路，综合考虑土壤水热条件、理化性状、微生物过程及根系周转等生物及非生物因子的变化，将有助于从机理上阐明土壤呼吸对冻融变化的响应规律。

（4）尽管研究者针对冻融期土壤呼吸的变化特征开展了一些探索性研究，但仍缺乏从土壤呼吸组分的角度探究土壤呼吸对冻融变化的响应机理。

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Review on the effects of freeze-thaw processes on soil respiration

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Abstract: A burst of soil respiration is often observed in high-altitude and high-latitude ecosystems during freeze-thaw period, and in some cases more than 50% of the annual emission of CO_2 from soils is found in the thaw period. Climate warming is expected to cause more frequent freeze-thaw events in these regions, which would enhance soil respiration and increase the contribution of soil respiration to ecosystem and regional carbon cycle. In this paper, we review the literatures involved in the effects of freeze-thaw processes on soil respiration. The stimulating effects of freeze-thaw events on soil respiration are related to extreme minimum temperatures at freezing, soil water content, the duration of soil freezing, and freeze-thaw cycles. Generally speaking, the lower the freezing temperature, the longer the freezing time, the higher the soil moisture content, the more likely the soil respiration will peak in the melting period, and the peaks would gradually die down with the increase of the numbers of freeze-thaw cycles. In addition, the depth, timing and duration of snow cover greatly influence the magnitude of soil CO_2 fluxes during freeze-thaw period. Changes in soil physical properties and aeration, root turnover (the death of roots), organic substrate availability, soil microbial activity and composition explain increased soil CO_2 fluxes following freeze-thaw events, but these involved mechanisms have seldom been addressed in detail. There is a lack of field studies on CO_2 emissions focusing on freeze-thaw effects and our knowledge on that topic is largely based on laboratory experiments. We discussed the limitations of current research methods and the directions for improvement: (1) the timing of soil collection should be coordinated with the season for which freeze–thaw cycles are being simulated. Clearly, simulations of freeze–thaw cycles at spring thaw should be performed on samples collected in the autumn and winter; (2) controlled manipulations of soil freeze–thaw cycles need to be redesigned to reduce large fluctuations in temperature below the soil surface and maintenance of realistic soil temperature fluctuations across the soil profile; (3) studies of freeze–thaw cycles should incorporate plant litter on the surface, as much of this carbon may influence soil microbial activity as it

leaches into the soil. Likewise, the effects of a melting snow layer should be incorporated into studies of freeze–thaw cycles, because soil moisture influences both freeze–thaw cycle frequency and the temperature distribution of soil; (4) the lengths of freeze–thaw cycles should be extended, and the number of freeze–thaw cycles should also be increased. Combined with the current research progress, the research emphases in the future are put forward as follows: (1) enhance the research involved in the effects of freeze-thaw processes on soil respiration on high altitude cold ecosystems; (2) combine field observations or in situ tests with laboratory simulation experiments, and further optimize the design of laboratory simulation experiments; (3) take into account the integrative effects of biotic and abiotic factors; (4) explore the response mechanisms of soil respiration to freeze-thaw fluctuations from soil respiration components and processes (autotrophic respiration and heterotrophic respiration).

Keywords: soil respiration; freeze-thaw fluctuation; stimulating effect; biotic factors; abiotic factors